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| Title | The presence of heterospecific males causes an Allee effect |
| Author(s) | Kyogoku, Daisuke; Nishida, Takayoshi |
| Citation | Population Ecology (2012), 54(3): 391-395 |
| Issue Date | 2012-07 |
| URL | http://hdl.handle.net/2433/159430 |
| Right | The final publication is available at www.springerlink.com |
| Type | Journal Article |
| Textversion | author |

**Title**: The presence of heterospecific males causes an Allee effect.

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**Number of text pages**; 12

**Number of figures and tables**: One figure and no table.

**Abstract**

The Allee effect is a positive causal relationship between any component of fitness and population density or size. Allee effects strongly affect the persistence of small or sparse populations. Predicting Allee effects remains a challenge, possibly because not all causal mechanisms are known. We hypothesized that reproductive interference (an interspecific reproductive interaction that reduces the fitness of the species involved) can generate an Allee effect. If the density of the interfering species is constant, an increase in the population of the species receiving interference may dilute the per capita effect of reproductive interference and may generate an Allee effect. To test this hypothesis, we examined the effect of heterospecific males on the relationship between per capita fecundity and conspecific density in *Callosobruchus chinensis* and *C. maculatus*. Of the two species, only *C. maculatus* females suffer reproductive interference from heterospecific males. Only *C. maculatus*, the species susceptible to reproductive interference, demonstrated an Allee effect, and only when heterospecific males were present. In contrast, *C. chinensis*, the species not susceptible to reproductive interference, demonstrated no Allee effect regardless of the presence of heterospecific

males. Our results show that reproductive interference in fact generated an Allee effect, suggesting the potential importance of interspecific sexual interactions especially in small or sparse populations, even in the absence of a shared resource. It may be possible to predict Allee effects produced by this mechanism *a priori* by testing reproductive interference between closely related species.

**Key words**

*Callosobruchus* • Depensation • Dilution effect • Frequency dependence • Interspecific interaction • Reproductive interference

## Introduction

The Allee effect is a positive causal relationship between any component of fitness and population density or size (Stephens et al. 1999). Allee effects have been broadly recognized as an important ecological phenomenon in conservation biology (Courchamp et al. 1999; Stephens and Sutherland 1999), biological invasion (Taylor and Hastings 2005; Liebhold and Tobin 2008), and biological control introductions (Hopper

54 and Roush 1993), because they can lead to the extinction of small or sparse populations.
55 Various mechanisms have been suggested to generate Allee effects, including
56 mate-finding difficulty, lack of predator satiation, and reduced foraging efficiency
57 (Courchamp et al. 2008). However, though some species are unlikely to suffer from an
58 Allee effect, other species with similar life history traits are subject to Allee effects (e.g.,
59 Myers et al. 1995; Drake 2005; Fauvergue et al. 2007). Thus, predicting which species
60 will be subject to an Allee effect remains a challenge. It is possibly because some of
61 Allee effects are caused by an as yet unknown mechanism.

62 We propose the novel hypothesis that reproductive interference can generate an
63 Allee effect, owning to its positive frequency dependence. Reproductive interference is
64 a negative interspecific sexual interaction that reduces the fitness of at least one of the
65 species involved (Gröning and Hochkirch 2008; Burdfield-Steel and Shuker 2011). For
66 example, when a male of species A mistakenly recognizes a female of species B as a
67 conspecific and attempts to mate with her, the female might suffer from an energy or
68 time loss, reduced opportunities to mate with conspecifics, gamete wastage, genital
69 damage, or hybrid formation (Gröning and Hochkirch 2008). Notably, in terms of its
70 effect on population dynamics, reproductive interference seems to show frequency
71 dependence (Kuno 1992; Gröning and Hochkirch 2008; Takakura et al. 2009): the

72 higher the frequency of species A, the greater the intensity of the reproductive
73 interference on species B. If for a pair of species, reproductive interference is
74 asymmetric (unidirectional) and the density of interfering species A is constant, the per
75 capita level of interference with the interfered species B should become diluted as the
76 density of species B increases. This dilution of reproductive interference should
77 generate an Allee effect when it is accompanied by increased fitness of species B. Thus,
78 reproductive interference may generate an Allee effect via a dilution effect, just as
79 predation does (Gascoigne and Lipcius 2004).

80 To test this hypothesis, we examined the relationship between per capita
81 fecundity and conspecific density when heterospecific males were present in a pair of
82 bean weevil species, *Callosobruchus chinensis* (Linnaeus) and *C. maculatus* (Fabricius).
83 Nishigaki (1963) measured copulation frequency in *C. chinensis* and reported that males
84 had difficulty in finding mates. In typical laboratory conditions, however, both *C.*
85 *chinensis* and *C. maculatus* show no positive relationship between population density
86 and lifetime reproductive success in isolation from the other (e.g., Yoshida 1966). Kishi
87 et al. (2009) showed that the fecundity of *C. maculatus*, but not that of *C. chinensis*, is
88 asymmetrically reduced when heterospecific males are present; thus, they show
89 asymmetric reproductive interference. We predict specifically that *C. maculatus*, the

90 species more susceptible to reproductive interference, will suffer an Allee effect only
91 when heterospecific males are present, and that *C. chinensis*, the non-susceptible species,
92 suffers no Allee effect.
93
94 **Materials and methods**
95
96 We used the jC-F strain of *C. chinensis* (see Harano and Miyatake 2005) and the hQ
97 strain of *C. maculatus* (see Miyatake and Matsumura 2004), both of which were derived
98 from the stock cultures of Okayama University. We chose these strains, because Kishi et
99 al. (2009) used these same strains to confirm unilateral reproductive interference by *C.*
100 *chinensis* on *C. maculatus*. The stock cultures were maintained under laboratory
101 conditions (25°C, 50–60% relative humidity, and 16L8D) and fed on adzuki beans,
102 *Vigna angularis* (Willd.) cv. Dainagon. Mated females of *C. chinensis* and *C. maculatus*
103 lay about 60 eggs on bean surfaces without feeding during their adult lifespan of around
104 10 days. Males of both species try to copulate with either heterospecific or conspecific
105 females indiscriminately even when conspecific females are present (Kishi et al. 2009).
106 Interspecific copulation is sometimes observed, but no hybrid has been reported
107 (Yamane and Miyatake 2010).

Virgin males and females of *C. chinensis* and *C. maculatus* were prepared for our experiments as follows. About 40 g of adzuki beans were placed in each of two plastic Petri dishes (ϕ90 mm × 20 mm). Then, about 10 females of each species were randomly chosen from the stock cultures (200-400 individuals in each generation), and allowed to lay eggs on the beans in one of the dishes. Beans with one, two, or three eggs on them were selected and placed individually in wells of a 24-well plastic plate (each well, ϕ15.5 mm × 17.3 mm). Beans with four or more eggs were discarded to avoid potential overcrowding effects. Each well was checked every day for newly emerged virgin individuals (i.e., individuals that emerged singly or in a unisexual group).

The effect of *C. chinensis* males on per capita fecundity (i.e., average number of hatched eggs per female) of *C. maculatus* was investigated under different *C. maculatus* density regimes as follows. From one to five *C. maculatus* pairs, each consisting of one male and one female individual, were housed with three *C. chinensis* males throughout their lives in a plastic Petri dish (ϕ70 mm × 15 mm) containing 9.0 g of adzuki beans. Before the two species were put together, we allowed each *C. maculatus* female to copulate with a conspecific male to exclude the possibility that the presence of heterospecific males would lead to a potential mate-finding difficulty. We introduced only male heterospecifics, rather than heterospecific pairs, because we

wished to investigate how reproductive interference by heterospecific males affected the fecundity of the *C. maculatus* females. As the control, we also examined the per capita fecundity of one to five pairs of *C. maculatus* housed without any *C. chinensis* males. After 20 days, by which time all females had died, we counted the number of hatched eggs in each experimental replication and control treatment (we performed 16 or 17 replications of each) in each density regime to determine the per capita fecundity of *C. maculatus* and the effect of reproductive interference by *C. chinensis* males. We similarly examined the effect of *C. maculatus* males on the relationship between fecundity and density in *C. chinensis*. All experiments were conducted at 25°C, 50–60% relative humidity, and 16L8D. We used analysis of covariance (ANCOVA) to examine the effects of the presence of heterospecific males, conspecific density, and their interactions on per capita fecundity. All statistical analyses were conducted with R software version 2.11.1 (R Development Core Team 2010). The significance level for the statistical tests was set at $P = 0.05$.

## Results

The presence of *C. chinensis* males significantly reduced the per capita fecundity of *C.*

144 *maculatus*, and the impact was greater when the density of conspecifics was lower
145 (ANCOVA: *C. chinensis* males, $F_{1,165} = 130.05$, $P < 0.001$; density, $F_{1,165} = 18.71$, $P <$
146 0.001; interaction, $F_{1,165} = 16.59$, $P < 0.001$; Fig. 1a). In contrast, in the absence of *C.*
147 *chinensis* males, density and fecundity of *C. maculatus* were not significantly related
148 (linear regression analysis: $F_{1,83} = 0.028$, $P = 0.87$; Fig. 1a). The presence of *C.*
149 *maculatus* males had no significant effect on per capita fecundity of *C. chinensis*, but *C.*
150 *chinensis* density had a significant negative effect on the fecundity of that species
151 (ANCOVA: *C. maculatus* males, $F_{1,164} = 0.56$, $P = 0.45$; density, $F_{1,164} = 8.81$, $P =$
152 0.003; interaction, $F_{1,164} = 2.79$, $P = 0.10$; Fig. 1b).
153
154 **Discussion**
155
156 We suggest that reproductive interference by *C. chinensis* generated an Allee effect in *C.*
157 *maculatus*. The presence of *C. chinensis* males reduced the per capita fecundity of *C.*
158 *maculatus* (Fig. 1a), a result in accordance with the findings of a previous study that
159 documented asymmetric reproductive interference by *C. chinensis* males on *C.*
160 *maculatus* females (Kishi et al. 2009). A higher density of *C. maculatus*, however,
161 mitigated the reduction in per capita fecundity, generating an Allee effect (Fig. 1a).

Although the presence of *C. chinensis* males reduced the per capita fecundity of *C. maculatus*, in the absence of *C. chinensis*, the fecundity of *C. maculatus* did not depend on density (Fig. 1a). Thus, we can attribute the observed fecundity reduction in *C. maculatus* exclusively to the presence of *C. chinensis* males. *Callosobruchus chinensis* males attempt to mate with females of either species indiscriminately (Kishi et al. 2009). In this study, the relative abundance of *C. chinensis* males to *C. maculatus* decreased as *C. maculatus* density increased. A single *C. maculatus* female was, therefore, expected to experience fewer mating attempts by *C. chinensis* males as the density of *C. maculatus* increased, as a result of the dilution effect. If this held true, the hypothesized reduction in the number of mating attempts by *C. chinensis* males can explain the enhanced per capita fecundity of *C. maculatus* with increasing *C. maculatus* density (Fig. 1a). We also observed no Allee effect in *C. chinensis*, which shows little susceptibility to reproductive interference by *C. maculatus*, a result consistent with our hypothesis (Fig. 1b).

The effects of the presence of heterospecific males on per capita fecundity were asymmetric; although *C. chinensis* males reduced the fecundity of *C. maculatus* (Fig.1a), *C. maculatus* males had no significant effect on the fecundity of *C. chinensis* (Fig. 1b). Interspecific copulation sometimes occurs between *C. chinensis* males and *C. maculatus*

females, but it seldom occurs between *C. maculatus* males and *C. chinensis* females (Yamane and Miyatake 2010). Thus, it is likely that the interspecific copulation between *C. chinensis* males and *C. maculatus* females plays an important role in the asymmetric reduction in fecundity. Yamane and Miyatake (2010), however, suggested that neither sperm nor seminal fluid was transferred during interspecific copulation between *C. chinensis* males and *C. maculatus* females. In *Callosobruchus*, male genitalia have spines, which injure the genital tracts of the females during intraspecific copulation (e.g., Crudgington and Siva-Jothy 2000; Rönn et al. 2007). The genital spines of *C. chinensis* males may thus injure the genital tracts of *C. maculatus* females, and the putative injury might cause the fecundity reduction in *C. maculatus*. Another possibility is interspecific sexual harassment. Though males of both species attempt to mate with heterospecific females (Kishi et al. 2009), some behavioral differences between these species may cause asymmetric fecundity reduction. Further experiments are necessary to find out whether structural damage or behavioral interference is actually responsible for the asymmetric reproductive interference between *C. chinensis* and *C. maculatus*.

In our experiments, difficulty in finding mates was eliminated by allowing females to copulate with a conspecific male prior to experiments, and reproductive interference generated an Allee effect in *C. maculatus* even with the presence of

198 conspecific sperm (Fig. 1a). However, reproductive interference may cause lack of
199 conspecific sperm. For example, heterospecific matting attempts may interfere with
200 conspecific copulations (Liu et al. 2007). Thus, without copulation with a conspecific
201 male prior to interaction with heterospecifics, the Allee effect might be enhanced. The
202 interaction between reproductive interference and conventional mechanisms of Allee
203 effects is an important topic for further research.

204 It is not clear to what extent reproductive interference causes Allee effects in
205 nature. The importance of reproductive interference as a mechanism generating an Allee
206 effect depends on the generality of reproductive interference itself. The role of
207 reproductive interference in population dynamics, however, has not been appreciated
208 until recently (Gröning and Hochkirch 2008). Reproductive interference is especially
209 likely when a biological invasion occurs (Burdfield-Steel and Shuker 2011), that is,
210 when originally allopatric species begin to interact with each other. Biological invasions,
211 therefore, may be one of the most promising settings in nature for finding an Allee
212 effect generated by reproductive interference. On the other hand, several studies have
213 documented reproductive interference between originally sympatric species (e.g.,
214 McLain and Pratt 1999; Hettyey and Pearman 2003; Van Gossum et al. 2007),
215 suggesting that it has the potential to produce Allee effects in sympatric species as well.

Allee effects are increasingly appreciated for their importance in applied ecology problems, such as conservation and biological invasion (Taylor and Hastings 2005; Courchamp et al. 2008; Tobin et al. 2011). Here we showed that reproductive interference can indeed generate an Allee effect. If reproductive interference can generate an Allee effect in nature, then programs dealing with small or sparse populations need to examine interactions between closely related species, even those that do not share a limited resource.

## Acknowledgements

We are grateful to T. Miyatake for providing the bean weevils. We thank N. Osawa, S. Noriyuki and S. Seiter for useful comments on our manuscript, and S. Oku for statistical advice. This study was partly supported by a Grant-in-Aid for Scientific Research (Ministry of Education, Culture, Sports, Science and Technology of Japan; No. 60208189) to TN.

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329

330 **Figure legend**

331

332 Fig. 1. Per capita fecundity of *C. maculatus* (a) and *C. chinensis* (b) in the absence

333 (open circles) or presence (closed circles) of heterospecific males, plotted against

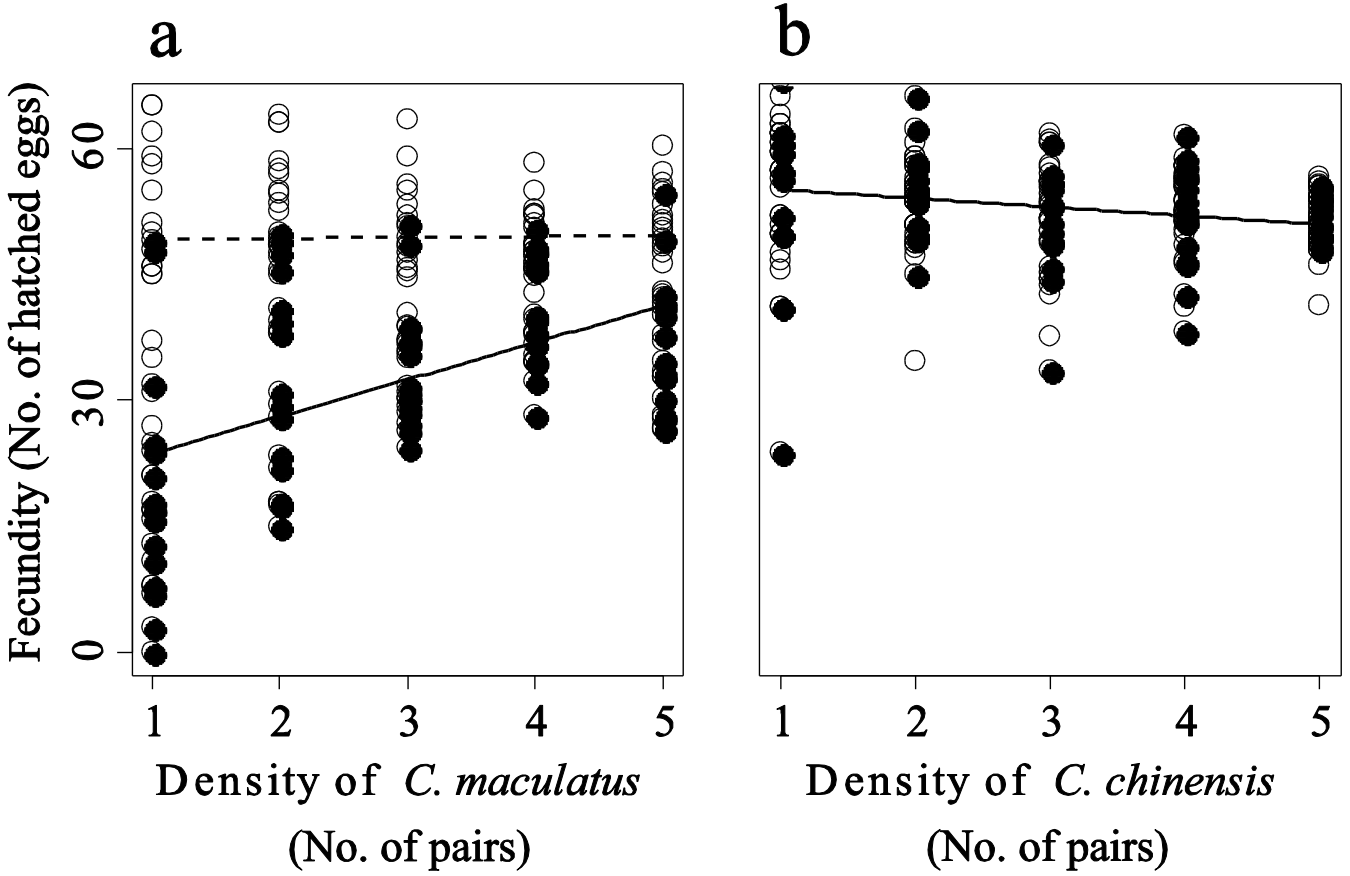
334 population density. In (a), the broken line and the solid line are regression lines for

335 the data in the absence or presence of *C. chinensis* males, respectively. In (b), the

336 regression was calculated using all data, because the effect of *C. maculatus* males

337 on *C. chinensis* fecundity was not significant.

Fig. 1.


a
b
Fecundity (No. of hatched eggs)
0
30
60
1
2
3
4
5
Density of C. maculatus
(No. of pairs)
Density of C. chinensis
(No. of pairs)